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Plant invasions as a biogeographical assay: Vegetation biomes constrain the distribution of invasive alien species assemblages

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ABSTRACT

Plant assemblages define vegetation patterns at different scales, from plant communities at the scale of small plots to broad biomes. Species assemblages are traditionally investigated with a focus on native species, and the spatial patterns and dynamics of alien species assemblages have received much less attention. Here, we explore the biogeography of a subset of invasive alien plants (IAPs) in South Africa and derive several "alien biomes" based on the alien plant assemblages and associated environmental drivers. We propose six hypotheses (the Weed-Shaped Hole; the Biome Decides; Goldilocks; a New World Order; Something In The Way You Move; and Random Tessellation) based on different drivers (disturbance, competition, climate, global change, introduction dynamics, and null respectively) that might explain distribution patterns. In particular, we explore whether invasive plant assemblages are controlled by the same fundamental factors that define native plant assemblages and biomes. A cluster analysis of the spatial distribution of 69 invasive alien plant species revealed five clearly delineated geographic clusters, three of them significantly aligned with the distribution of vegetation biomes (fynbos, grassland and savanna). The major determinants of the distribution of IAP clusters were identified based on a classification tree analysis. We found that broad environmental variables, especially vegetation biomes, explained the distribution of IAP clusters (60% classification accuracy). We could not find a strong relationship with anthropogenic factors, such as land cover or anthromes, even at a finer scale. Our results indicate that vegetation biomes are characterised by hard environmental barriers which also constrain the distribution of IAPs in South Africa. This supports the development of biome-level strategies for the control of alien plant species in South Africa.

1. Introduction

Humans have intentionally or accidentally moved organisms around the world for many centuries (Elton, 1958). This has resulted in many species establishing self-sustaining populations outside their native ranges, i.e. in regions separated from the native ranges by substantial biogeographic barriers. The human-mediated reshuffling of the world's biota has intrigued researchers for many decades, especially the last few decades (Thuiller et al., 2006; Van Kleunen et al., 2010a; Richardson, 2011). Many introduced species have become invasive and can have detrimental effects in recipient ecosystems (e.g. Gaertner et al., 2009; Vilà et al., 2011). Understanding the patterns and drivers of alien species distributions, especially invasive species, is critical to inform management strategies.

Many aspects of the biogeography and ecology of biological invasions have been well studied (Pyšek and Richardson, 2006; Van Kleunen et al., 2010b; Richardson, 2011). However, the spatial patterns and dynamics of alien species assemblages (i.e. how alien species assemble and co-occur across landscapes) have received much less attention (but see Pyšek et al., 2005; Hui et al., 2013). Species assemblages are traditionally investigated with a focus on native species. Indeed, alien species are often considered "background noise" in such studies and are therefore ignored.

Plant assemblages define vegetation pattern at different scales—from plant communities at the scale of small plots to biomes at a regional level. Understanding vegetation pattern, through classification or ordination, has helped to unpack the drivers of vegetation change and predict the impacts of human activities on vegetation

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patterns (Chytrý et al., 2011). Several approaches have been proposed to classify vegetation based on one or several factors which include physiognomy, structure, species composition, soil or climatic conditions. Although there is no universally accepted classification scheme, vegetation types provide a useful tool for basic and applied research (Kent, 2011; De Cáceres and Wiser, 2012). Biomes are typically defined on the basis of broad vegetation types and the biophysical features that exercise fundamental control on the distribution of plants (O'Neill, 1986; Cox and Moore, 2000). Assemblages of native plants are mediated by direct and indirect biotic interactions over evolutionary time scales. However, invasive alien plants (IAPs) now dominate vegetation in many parts of the world, and so it is important to know whether the same rules apply to *assemblages* of invasive plants—do they cluster in predictable ways?

IAPs are recent arrivals, and their distribution and abundance can usually be explained by assessing life-history traits and their interactions with elements of the introduction history, notably aspects of introduction and dissemination pathways such as propagule pressure, the level of exposure to potentially invasible ecosystems and residence time (Wilson et al., 2007; Richardson et al., 2011, 2014). Such determinants have typically exercised influence over relatively short time scales—decades to centuries. In addition, the widespread alteration of ecosystems by humans caused by agriculture, urbanisation and other land uses has led to the formation of globally-significant ecological patterns. Anthropogenic biomes ('anthromes') have been defined to reflect this new ecological order (Ellis and Ramankutty, 2008). As such, the distribution of invasive species might be expected to follow the distribution of anthromes.

One of the fundamental reasons underlying the success of some invasive species is the lack of a shared evolutionary history with the components of recipient ecosystems (Cox, 2004). Many invasive species have dramatically altered many features of invaded vegetation (South African examples include: Yelenik et al., 2007; Iponga et al., 2008; Van Wilgen et al., 2008; Gibson et al., 2012). There is, however, little understanding of how assemblages of alien plants are collectively affected by biotic and abiotic features. Biological invasions can be used as a natural experiment for exploring the determinants of vegetation boundaries—as a bioassay. However, a complicating factor is that few, if any, invasive species have sampled all potentially invasible habitats in their introduced ranges—it is for this reason that the roles of traits and introduction histories typically override those of the fundamental biological processes in shaping the distributions of invasive alien plants (Thuiller et al., 2006 and Wilson et al., 2007).

Many taxa in South Africa's introduced plant flora were introduced to the region more than two centuries ago and have been widely disseminated within the region. Although many of these species have yet to occupy all environmentally suitable areas (Rouget et al., 2004), such species arguably provide an intriguing opportunity to test whether invasive plant assemblages are controlled by the same fundamental factors that define native plant assemblages and biomes. As far as we know, invasive species have yet to be used as a "bioassay" in this way, and South Africa provides a good opportunity for testing the utility of this approach. We explore the biogeography of a subset of invasive alien plants in South Africa and derive several "alien biomes" based on the current alien plant assemblages and associated environmental drivers. This work builds on previous studies by Richardson et al. (2004) and Hugo et al. (2012) who investigated aspects of alien plant species assemblages in South Africa. We provide a more detailed analysis and test several hypotheses to explain the observed biogeographic patterns. In particular we explore the role of vegetation biomes and spatial scale in shaping the spatial patterns of alien plants in South Africa. To this end we propose six hypotheses to explain the current distribution of invasive plant species in relation to vegetation biomes (Table 1). We suggest ways of testing each hypothesis based on the spatial pattern of alien plant species and highlight implications for understanding and management (Table 1).

2. Materials and methods

2.1. Data source

Distribution records of invasive plant species (IAPs) were obtained from the Southern Africa Plant Invader Atlas (SAPIA; Henderson, 1998 and see also Richardson et al., 2005 for further details). SAPIA is the most comprehensive source of data on the distribution of IAPs in South Africa. IAPs invading natural areas have the greatest ecological impacts (Richardson and Van Wilgen, 2004). In this study, we focused on the drivers of the distribution of terrestrial alien species invading natural habitats. We therefore removed records occurring in "transformed habitats" from the database (e.g. gardens, cultivated areas); and only used records from natural and semi-natural terrestrial habitats. Species with <50 records were ignored. This resulted in a total of 69 species. Most of the species included in this analysis have a large residence time (at least 50 years, with a median value of 150 years) which provided ample opportunities for the species to establish and spread throughout their suitable habitat.

To test the effect of spatial scale, two datasets of varying spatial resolution were compiled: one at a 15-minute resolution (9432 presence/absence records in 1281 grid cells, up to 34 species per cell, with a median value of 5 species) and the other at a 5-minute resolution (13,602 presence/absence records in 2915 grid cells, up to 26 species per cell, with a median value of 4). All duplicate records of the same species in the same grid cell were removed, hence there were fewer records in the 15-minute resolution dataset than in the 5 minute one. We hypothesised that the drivers of invasions might differ depending on the spatial scale of investigation. From our proposed hypotheses (Table 1), we assumed that broad-scale environmental drivers (such as those that have shaped biomes) would be more important at a broad-scale (i.e. 15 min) whereas anthropogenic drivers and possibly competition would explain better the distribution of IAPs at finer scales (i.e. 5 min; see Rouget and Richardson, 2003 for discussion).

To test our hypothesis of random tessellation, a null model of alien species distribution was generated. The null model retained the number of records and their spatial autocorrelation for each species. Specifically, we first calculated the occupancy and spatial correlation of each species (Hui et al., 2006) and then estimated the colonisation rate of each species under a constant local extinction rate (=0.05) using the pair approximation of the patch occupancy metapopulation model (Hui and Li, 2004; Hui, 2011). Finally, we ran a cellular automaton for each species based on estimated colonisation rate and randomly assigned introduction location (e.g. Roura-Pascual et al., 2009; Caplat et al., 2014; Donaldson et al., 2014). We ran the model at the 15-minute resolution to mitigate the influence of linear sampling scheme for data capture (along roads).

To test the hypothesis that IAP clusters correlate with vegetation biomes, we used the vegetation biomes dataset from Mucina and Rutherford (2006). This dataset represents the original distribution of 10 large ecological zones defined on the basis of vegetation structure and climate. These are (in descending order of extent): Savanna (covering 32% of South Africa), Grassland (26%), Nama Karoo (20%), Fynbos (7%), Succulent Karoo (7%), Azonal vegetation (2%), Albany Thicket (2%), Indian Ocean Coastal Belt (1%), Desert (<1%) and Forest (<1%).

To test the hypothesis that IAP clusters correlate with anthropogenic factors, we used the anthromes dataset for Africa (Ellis and Ramankutty, 2008) and the 2009 national land cover (SANBI, 2009). The anthrome dataset represents 19 anthromes in South Africa that are defined on the basis of major anthropogenic activities that affect vegetation. The national land cover represents seven broad land-use classes for each 1-minute pixel.

We also used elevation and eight climatic factors from the South African Agro-Climatic Atlas (described in Schulze et al., 1997) that are known to be associated with plant species distribution (Rouget et al., 2004). These include mean annual temperature, mean annual

Table 1
Hypotheses to explain the current distributions of invasive alien plant (IAP) species. The hypotheses vary in the degree to which IAP distributions are expected to correspond to biomes defined on the basis of native plant assemblages. The hypotheses also vary in the importance of propagule pressure, abiotic characteristics, biotic characteristics, and human influence of humans (Catford et al., 2009).

Hypothesis	Main driver of pattern	Description	Expected patterns/supporting evidence	Implications for understanding and management
1: "The weed-shaped hole"	Disturbance (Abiotic)	Invasions are facilitated by certain levels of disturbance; these may be anthropogenic or natural (and so an inherent function of the invasibility of an ecosystem) (Mack et al., 2000; Buckley et al., 2007)	IAP species clustering tends to follow anthromes and/or biomes where fire is a key driver of ecosystem dynamics (fynbos, savanna and grassland) Current distributions of IAPs are largely a function of the spatial patterns of disturbance regimes	Disturbance is a main factor in allowing IAP populations to establish and spread. Need to focus on managing disturbance regimes to control invasions, or plan management actions around disturbance events
2: "The biome decides"	Competition (Biotic)	Biomes differ inherently in invasibility, such that there is selectivity regarding which invasive species can and cannot invade (Alpert et al., 2000).	IAP species clustering will correspond with biome boundaries, with some invasive species negatively associated with certain biomes despite opportunities for such species to invade and seemingly suitable physiological conditions.	Provides insights on how species interact and coexist within biomes. Given the importance of context and species interactions, it might be expected that invasiveness elsewhere in the world would be a less important driver. There might be a large difference between taxa observed to be invasive in transformed areas from those that invade natural ecosystems. Need to separate strategic plans for IAP risk assessment and management for each biome
3: "Goldilocks"	Climate (Abiotic)	Biomes and invasive species share broadly similar abiotic requirements, such that they occupy the same niches	IAP species clusters will correspond to particular climatic niches (e.g. Rouget et al., 2004). Expect natural biome boundaries to also follow climatic boundaries, and potentially biomes in different parts of the world show similar climatic boundaries.	Insights on environmental factors limiting the spread of IAPs. Bioclimatic models of species distributions based on native ranges will provide accurate estimates of potential ranges in new regions. Management should be based on climatic zones and expect shifts in invasion with changing climate.
4:"A new world order"	Global change (Humans)	A new set of boundaries are formed by suites of interacting native and alien species (O'Dowd et al., 2003; Green et al., 2011). These new associations lead to novel ecosystems that need not be similar in nature to those in previous biomes.	Invasions cluster together though not in relation to factors mentioned above. New boundaries are formed but IAP clusters do not correspond with biomes. Likely to see invasional meltdown.	The concept of a "biome" will have little meaning for IAPs, but how such novel ecosystems form will provide insights on a potentially new set of drivers of distributions. It will be hard to predict the trajectories of invasions, and might need to manage novel ecosystems or species on a case by case basis.
5: "Something in the way you move"	Introduction dynamics (Propagule pressure)	Distribution patterns in invasions are dominated by drivers associated with introduction histories of IAPs (Wilson et al., 2009; Donaldson et al., 2014).	Species over-represented close to points of introduction; and human activities. Species clustering tend to follow anthromes. These patterns may be expected to decrease as residence time increases, i.e. the "settling-down" hypothesis (Hui et al., 2013), but equally such initial stochasticity might last, leading to novel ecosystems (see above).	Current distribution patterns are strongly influenced by historical socio-economic forces and so require a multi-disciplinary approach. Current invasive distributions are likely to be poor predictors of future (or potential) distributions. Control should focus around points of introductions and historical and future pathways.
6: "Random tessellation"	Geometry (none)	The distributions of IAP species is inherently idiosyncratic (Daleo et al., 2009). When many species are considered it appears that the relative clustering of distributions are simply constrained by geometry.	There will be no significant correlation to any individual biotic or abiotic variables. Clustering patterns will correspond to a null model where distributions are allocated randomly to the map with the constraint that overall distributions in extent and arrangement are preserved for each species. Different levels of species clustering no different from null models, though such clustering may, at first glance, look as though patterns are present	Each species must be studied and managed individually and no particular mechanistic clustering of distributions.

precipitation, growth temperature, number of growing days, minimum soil water stress, average temperature of the coldest month, average temperature of the hottest month, and number of frost days.

2.2. Species clustering—alien biomes

A cluster analysis of grid cells (15-minute or 5-minute resolution) was performed based on the presence/absence of invasive alien plant species per cell to identify geographic clusters. In other words, grid cells were clustered together if they share similar species composition. No other factor was included; clustering is based simply on the presence/absence of invasive alien plant species. We first transformed the raw data matrix using Hellinger transformation (see Legendre and Gallagher, 2001) and then applied a K-means algorithm based on Euclidean distances of the transformed data. Such clustering method is suitable for the presence/absence datasets as it assigns low weight to rare species while preserving a Euclidean distance (Legendre and Gallagher, 2001). We selected a similar number of clusters as the number of biomes (6 large biomes in South Africa) and the results are presented based on six clusters.

We generated three sets of clusters: 1) with the distribution of IAPs at 15-minute resolution from SAPIA; 2) with the random-generated distribution of IAPs (null hypothesis); and 3) with the distribution of IAPs at 5-minute resolution from SAPIA. Each grid cell was then assigned to a cluster to derive maps of the different clusters obtained. For each cluster, the dominant/characteristics species were identified. Characteristic species were defined as those with more than 50% of their distribution within one cluster.

2.3. Analysis of potential drivers

To determine which factors possibly drive the spatial patterns of alien clusters, we used a classification tree to predict cluster affiliation of grid cells (15 and 5 minute resolution). Other statistical approaches could be used but classification trees are a simple, non-parametric and intuitive technique for identifying possible drivers. The following potential predictors were considered, aligned with the major hypotheses that were tested: climate (average value per grid cell for 8 climatic variables), elevation, vegetation biomes (dominant biome per grid cell—categorical variable), anthromes (dominant anthrome per grid cell), land cover (dominant land cover per grid cell), and degree of habitat conversion (% of each grid cell occupied by urban and agricultural areas). Classification trees were calibrated based on 70% of the records, and the remaining records were used to validate the model and to determine the classification accuracy (based on error matrix between predicted and observed cluster values).

We then used the environmental factors associated with each geographic cluster, as identified by the classification tree, to predict the potential distribution of each invasive alien cluster. This represents the full potential distribution of alien species assemblages, which we referred to here as "alien biomes". The predictions were based on the 1 minute data of the environmental variables.

3. Results

At a broad spatial scale (15-minute resolution), the cluster analysis revealed six groups, five of which with well-defined boundaries (Fig. 1A). Clusters were characterised by distinct suites of species. Of 69 species (15-minute resolution), 51 occurred predominantly in only one cluster (more than 50% of grid cells occupied within one cluster) and three species occurred exclusively in one cluster: *Chromolaena odorata* in Cluster 5 and *Acacia pycnantha* and *Hakea drupacea* in Cluster 6. Characteristic species of each cluster are listed in Table 2.

The spatial pattern of IAP clusters was largely explained by climate. Although we included all potential predictors in the analysis, the resulting classification tree did not include anthromes. This classification tree, with the following variables, elevation, biome, number of frost days, growth days, mean temperature of the coldest month, mean annual temperature and mean temperature of the hottest month, yielded a validation accuracy of 65%. By excluding elevation and climatic factors, a much simpler classification tree was obtained which includes a combination of natural biomes and anthromes and yielded an accuracy of 60% (Fig. 2). At this resolution, broad-scale biophysical factors (such as regional climate and biomes) explained the spatial pattern obtained, followed by anthropogenic factors. Cluster 6 was tightly aligned with the distribution of the Fynbos biome, while clusters 1 and 5 had similar distributions to the Grassland and Savanna/Indian Ocean Coastal Belt biomes respectively (Fig. 1A). We therefore rejected hypotheses 1, 4 and 5 and our results support hypotheses 2 and 3.

As expected, the random-generated distribution of IAPs did not reveal any apparent clusters. The classification tree did not identify any meaningful variables explaining the spatial pattern and the classification accuracy remained low (39%).

At a fine scale (5-minute resolution), alien plant assemblages did not form very distinct geographic clusters (Fig. 1B) and differ from the geographic clusters obtained at coarser resolution (Fig. 1A). Only two clusters were closely associated with clusters derived at coarser resolution (15 minute). These corresponded to the clusters overlapping with the Fynbos and Grassland biomes. Of the 5-minute clusters, 74% of cluster F overlapped with cluster 5 at 15-minute resolution (Fig. 1) and 71% of cluster E overlapped with cluster 1 at 15-minute resolution. The other clusters, however were characterised by similar species (see supporting information).

The spatial pattern of IAP clusters at a 5-minute resolution could also be partly explained by vegetation biomes with a classification accuracy of 50%. Other variables did not significantly improve the classification accuracy. We therefore rejected the hypothesis related to anthropogenic drivers.

Based on the full classification trees of the alien invasive clusters at a 15 min resolution, we projected the potential distribution of each cluster (Fig. 3). These represent the full geographic range each alien species assemblage ("alien biomes") could occupy.

4. Discussion

This study explored the geographic distribution of alien species assemblages and their possible drivers. We found clear geographic clusters of invasive plant species at both spatial scales that were considered. This was rather surprising as the cluster analysis considered no spatial dimension, but only the co-occurrence of IAPs. Previous studies (Hugo et al., 2012) identified much more diffuse clusters. IAPs in South Africa seem to occupy different regions, co-occurring with a well-defined group of species (indicated by the high number of characteristic species per cluster).

We proposed six major hypotheses to explain the observed species assemblages of invasive plant species. Based on our analyses, we rejected those related to anthropogenic factors and/or random assemblage of species as the distribution of IAP clusters was largely constrained by vegetation biomes (Figs. 1 and 3). Although anthropogenic drivers clearly play a crucial role in the establishment and spread of alien species (Pyšek and Richardson, 2006 and Pyšek et al., 2010), the broad distribution and assemblages of alien species were largely constrained by broad environmental factors (the same ones that define the biomes based on native vegetation). These broad environmental factors seem to operate as barriers, dividing the environmental space into distinct clusters where native and alien species cannot easily cross cluster boundaries. Strong edaphic interfaces and contrasting disturbance regimes often define biome boundaries, such as between fynbos and other adjacent biomes, and largely explain species diversity and endemism among biomes (Cowling and Pressey, 2001 and Rouget et al., 2003). Similar factors might constraint the distribution of IAP species in South Africa. What wasn't clear was whether the biome boundaries

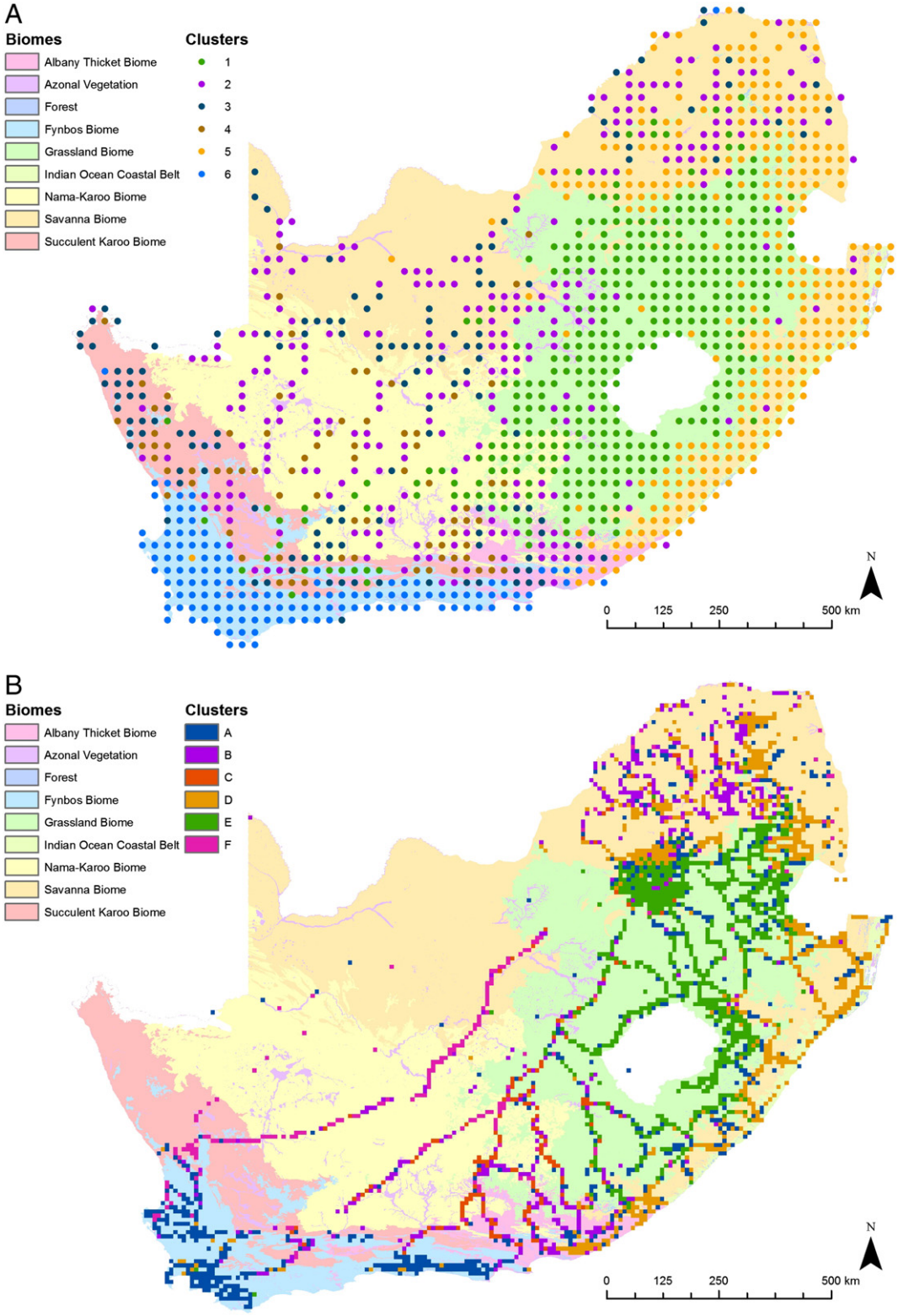

Fig. 1. Invasive alien species clusters in relation to natural vegetation biomes (shading). Clusters were derived based on presence/absence of invasive alien species in A) 15 minute grid cells (shown as circles); or B) 5 minute grid cells (shown as squares). The spatial resolution did not make much difference to the qualitative results, though when viewed as 5 minute grid cells it is clear that most of the sampling was based on observations made at the road-side (see Richardson et al., 2005).

drive the IAP distribution patterns (the "Biome Decides" Hypothesis) or whether the both alien species and native species respond to the same external drivers (the "Goldilocks" Hypothesis). This will require much finer scale distributional data and additional multivariate analysis (such as co-correspondence analysis and structural equation modelling) to contrast cases where IAPs have invaded natural ecosystems vs. only transformed ecosystem (e.g. Moodley et al., 2014 and Richardson et al., 2010).

Although there was little indication that current distributions are primarily shaped by introduction dynamics, the patterns observed

Table 2
Characteristics of clusters of invasive alien plant species (15-minute resolution, see Fig. 1a). Characteristic species have more than 50% of their occurrence in one cluster (listed in decreasing order) and unique species only occur in one cluster.

Cluster	Major biome	Characteristic species	Unique species
1	Grassland	*Populus nigra, Rosa rubiginosa, Pyracantha angustifolia, Gleditsia triacanthos, Salix fragilis, Robinia pseudoacacia, Cirsium vulgare, Populus deltoides, Populus alba, Acacia decurrens, Verbena bonariensis, Populus × canescens, Prunus persica, Acacia dealbata*	
2	Nama Karoo & arid Savanna	*Prosopis glandulosa* (recent research has shown that most of the invasive stands of *Prosopis* in South Africa are hybrids between *P. glandulosa* and other species; Mazibuko, 2012)	
3	Succulent Karoo & arid Savanna	*Nicotiana glauca*	
4	Succulent Karoo & Nama Karoo	*Atriplex nummularia*	
5	Savanna & Indian Ocean Coastal Belt	*Cardiospermum grandiflorum, Caesalpinia decapetala, Senna didymobotrya, Psidium guajava, Solanum seaforthianum, Pereskia aculeata, Lantana camara, Jacaranda mimosifolia, Cestrum laevigatum, Solanum mauritianum, Agave sisalana, Opuntia monacantha, Xanthium strumarium, Morus alba, Melia azedarach, Rubus cuneifolius, Sesbania punicea, Ricinus communis, Cereus jamacaru, Pinus patula, Salvinia molesta*	*Chromolaena odorata*
6	Fynbos	*Paraserianthes lophantha, Pinus pinaster, Eucalyptus conferruminata, Pinus radiata, Acacia saligna, Hakea sericea, Acacia cyclops, Rubus fruticosus, Acacia longifolia, Quercus robur, Acacia melanoxylon, Pinus halepensis*	*Acacia pycnantha, Hakea drupacea*

here might still be transient, with the spatial distribution and spread of future invasive species influenced by different drivers. Furthermore, the observed patterns and the role of macro-environmental factors such as biomes might not hold at finer spatial resolution, where propagule pressure and invasion pathways are often more important in explaining the distribution of IAPs (Rouget and Richardson, 2003; Von Holle and Simberloff, 2005). However, the lack of fine-scale distribution data on the distribution of invasive species limited our ability to explore this.

The role of natural disturbances such as fire and grazing was not explicitly considered in this study. It is difficult to disentangle the broad environmental characteristics of each biome (such as vegetation structure, soil and climate) from the suite of natural disturbances in each biome. Fire and grazing are a key component of the Fynbos, Grassland and Savanna biome (Bond, 2008; Kraaij and Van Wilgen, 2014). It is perhaps not surprising that the three IAPs clusters most associated with vegetation biomes (see Fig. 1A clusters 1, 5 and 6) are those where fire is a dominant driving force. Therefore we could not clearly determine the extent to which invasions are influenced by disturbances (Hypothesis 1, Table 1) or whether biomes differ inherently in their invasibility (Hypothesis 2, Table 1).

The spread of invasive alien species can result in biotic homogenisation where the native biodiversity is suppressed and replaced by widespread invasive species (McKinney and Lockwood, 1999). Fig. 3 shows the full extent that alien species assemblages could occupy in South Africa. As such, they depict potential alien biomes, resulting from biotic homogenisation. One would therefore expect novel ecosystems to form in these biomes based on the species assemblages listed in Table 2. Predicting the current and future impacts of invasive species is a challenging task (Kumschick et al., 2012; Blackburn et al., 2014). Most current frameworks for assessing the impact of biological invasions tend to be species-specific (i.e. each alien species is scored separately) making it difficult to quantify the cumulative impacts of invaded areas, as these are rarely invaded by one species. Knowing alien species assemblages and potential alien biomes, as identified here, might provide a starting point for assessing the cumulative impacts of groups of invasive species.

Understanding how alien species would shape in future natural ecosystems has important management implications. Our study indicates that strategies for alien plant control should be biome-specific. However, almost all the 368 IAP taxa regulated on continental South Africa are regulated the same across the whole country. Of the 50 or so that specify

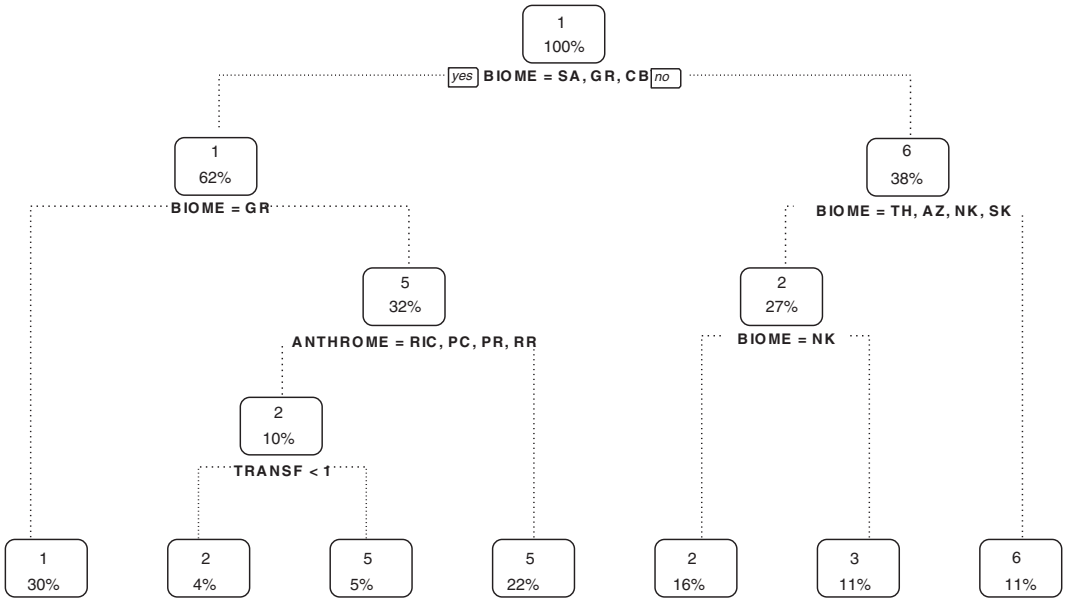

Fig. 2. Classification tree analysis of invasive alien species clusters (based on 1295 records at 15 minute resolution). Most clusters could be explained by a combination of biomes and anthromes. For each node (black-outlined box), the assigned cluster is indicated as well as the % of records. The most significant variable is indicated below each node, with the corresponding values for the left branch. Biome codes are: Savanna (SA), Grassland (GR), Indian Ocean Coastal Belt (CB), Albany Thicket (TH), Azonal vegetation (AZ), Nama Karoo (NK), and Succulent Karoo (SK). Anthromes codes are: Residential Irrigated Croplands (RIC), Populated Croplands (PC), Populated Rangelands (PR), and Remote Rangelands (RR). Transf = % of the 15 minute grid cell being transformed by urban or agricultural areas.

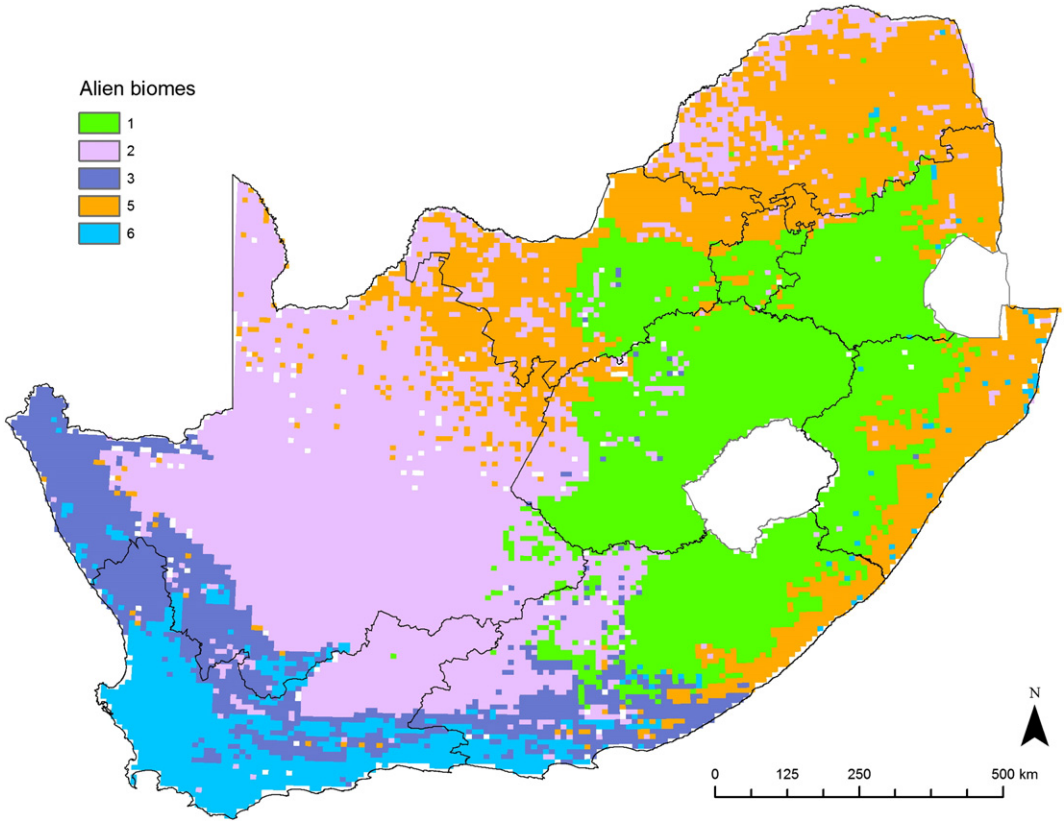

Fig. 3. Potential distribution of alien biomes. Environmental determinants of the distribution of invasive alien species clusters were identified from a classification tree (Fig. 2) and mapped over the full range of environmental factors in South Africa. Each alien biome is characterised by unique alien species assemblages (see Table 2 for characteristic and unique species for each cluster).

some geographical variation in regulation, almost all are defined by provinces, and only the listings for *Eriobotrya japonica* (Thunb.) Lindl. and *Eucalyptus spp.* make explicit reference to biomes (DEA., 2014). The evidence presented here suggested that the use of biome classifications makes much more ecological sense, though would be administratively complex. Crucially any attempts to make the regulations more geographically explicit, should not, however, conflict with the need for managing pathways and species. Often there is great uncertainty in the risks posed by species that are not yet widespread, due to either a short residence time or a limited number of initial introductions. Such species should likely still be assessed and pro-actively managed on a species by species basis (Wilson et al., 2013). Moreover, while biome-specific management will likely be an important and valuable step, it will also be important to understand the mechanisms behind the patterns. We suspect that future research looking to see whether biomes are the drivers of IAP distributional patterns or simply correlated to them (i.e. the Biome Decides Hypothesis vs. the Goldilocks Hypothesis) has the potential to significantly improve our management of the risks that invasions pose.

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Appendix A. Supplementary data

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